

REVIEW AND SYNTHESIS

The role of seasonal timing and phenological shifts for species coexistence

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Abstract

Shifts in the phenologies of coexistence species are altering the temporal structure of natural communities worldwide. However, predicting how these changes affect the structure and long-term dynamics of natural communities is challenging because phenology and coexistence theory have largely proceeded independently. Here, I propose a conceptual framework that incorporates seasonal timing of species interactions into a well-studied competition model to examine how changes in phenologies influence long-term dynamics of natural communities. Using this framework I demonstrate that persistence and coexistence conditions strongly depend on the difference in species' mean phenologies and how this difference varies across years. Consequently, shifts in mean and interannual variation in relative phenologies of species can fundamentally alter the outcome of interactions and the potential for persistence and coexistence of competing species. These effects can be predicted by how per-capita effects scale with differences in species' phenologies. I outline how this approach can be parameterized with empirical systems and discuss how it fits within the context of current coexistence theory. Overall, this synthesis reveals that phenology of species interactions can play a crucial yet currently understudied role in driving coexistence and biodiversity patterns in natural systems and determine how species will respond to future climate change.

Keywords

Climate change, coexistence, community dynamics, competition, mismatch, phenology, priority effect, seasonal variation.

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INTRODUCTION

Ecological communities are shaped by two fundamental axes: space and time. Although ecologists have long recognized that species interactions are constantly varying over time (Elton 1927; Hutchinson 1961), the traditional approach to community ecology has largely focused on space and taken a fairly temporally static view of species interactions (Wolkovich *et al.* 2014). For instance, classical Lotka-Volterra type competition, predation, and food web models allow number of individuals to vary, but traits such as per-capita interaction coefficients are typically assumed to be constant (i.e., time invariant). This simplification clearly contrasts with nature where life history traits and species interactions are highly seasonal and constantly change over time with changes in phenologies and environmental constraints (Dunbar *et al.* 2009; Yang & Rudolf 2010; Diez *et al.* 2012; Wolkovich *et al.* 2014). Furthermore, climate change is constantly modifying the temporal structure of species interactions (Nakazawa & Doi 2012; Wolkovich *et al.* 2014; Kharouba *et al.* 2018), which challenges many of the core assumptions of fundamental concepts and models in ecology. Indeed, accounting for temporal fluctuations can be essential to predict species coexistence and community structure (Chesson 2000; Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.* 2012). Consequently, there is a pressing need to build a temporally explicit framework that

explicitly accounts for the seasonal structure of species interactions to predict dynamics and structure of natural communities in a changing world.

Most species interactions are highly seasonally structured: the phenology of a species determines when and at what stage or size individuals interact with other members of the community (Yang & Rudolf 2010). For instance, a tadpole that hatches first within a growing season will initially face smaller and fewer interspecific competitors than a tadpole that hatches mid-season. Thus, the various phenologies of constituent species within a community define a 'timetable' that describes the days when interactions are initiated and when they end for all species interactions within a community within a given year. However, the seasonal timing of interactions is not fixed, but rather naturally varies across years (e.g., due to fluctuations in local weather conditions) (Singer & Parmesan 2011; Diez *et al.* 2012). Furthermore, climate change is altering the timing and temporal overlap of interacting species worldwide, leading to non-stationary (directional) changes in timing of interactions in aquatic and terrestrial systems across a wide range of taxa and types of interactions (Walther *et al.* 2002; Parmesan & Yohe 2003; Parmesan 2006; Durant *et al.* 2007; Thackeray *et al.* 2016; Cohen *et al.* 2018). Despite recent advances emphasizing the importance of timing for key coexistence mechanisms (Godoy & Levine 2014), it remains unclear how changes in the timing of species

interactions influence the long-term dynamic and structure of communities, species coexistence, and maintenance of biodiversity (Forrest & Miller-Rushing 2010; Wolkovich *et al.* 2014; Visser 2016).

The importance of the temporal co-ordination of phenologies for species interactions and community dynamics can be understood in the framework of seasonal community assembly. Each year, many temporary communities are largely reassembled anew: the appearance of new offspring in seasonal habitats represents annual cycles of habitat re-colonization, followed by periods where individuals grow and interact with each other. For example, many pond assemblages are reconstituted each year as terrestrial adults (e.g., insects, amphibians) return to ponds to breed, and aquatic stages of their life cycles interact during their ontogeny. Similar annual recolonization events occur in annual plant communities where the timing of germination from a seedbank determines the 'arrival' of individuals in the community, and many other temporary systems. The relative phenologies (e.g., timing of breeding, hatching, emergence from dormancy or germination) of species determine in what sequence species' offspring arrive in the community in a given year (e.g. Godoy & Levine 2014). Furthermore, phenologies vary naturally across years and sites leading to interannual variation in relative timing of species interactions (Høye & Forchhammer 2008; Thackeray *et al.* 2016; Rudolf 2018) and this variation is likely to increase with climate change (Pearse *et al.* 2017). Recent studies indicate that even small changes in the timing of species interactions can result in substantial changes in the outcome of species interactions (Stier *et al.* 2013; Godoy & Levine 2014; Rasmussen *et al.* 2014; Cleland *et al.* 2015; Young *et al.* 2015; Murillo-Rincón *et al.* 2017; Rudolf 2018; Alexander and Levine, 2019). This implies that per-capita interaction strengths are typically not constant, but instead naturally change over time with shifts in the relative phenologies of interacting species within and across years (e.g., Fig. 1). It is unclear, however, when we can safely ignore this variation (e.g., as in classical Lotka-Volterra type models and food webs) and when we need to account for the seasonal timing of interactions to avoid erroneous conclusions and predictions. Temporal variation in environmental conditions that influence the fitness of competing species (e.g., temporal storage effect) can play a key role in determining coexistence patterns (Chesson 2000; Barabás *et al.* 2018). Variation in the temporal co-ordination (phenology) of species interactions could be similarly important and act as a ubiquitous, but currently overlooked driver of species coexistence and biodiversity patterns. However, we still lack a general theoretical framework that incorporates these empirical patterns into existing community models to examine and predict the long-term effects of this temporal co-ordination in interactions.

To help fill this conceptual gap I propose a general theoretical framework that links shifts in relative seasonal timing of interactions (phenologies) and interannual variation in relative phenologies to well-studied competition models. Specifically I focus on a well-studied competition system to study when and how different aspects (i.e., mean and variance) of temporal changes in the timing of species interactions are expected to alter persistence and extinction rates of competing species and coexistence conditions.

Integrating seasonal timing and phenological shifts into community models

To examine the consequences of changes in the mean and variation of species' phenologies across years we can incorporate shifts in the timing of species interactions into classical time discrete community models in two steps. First, we describe population dynamics and species interactions within a year (i.e., seasonal) by modelling per-capita interaction strength as a function of relative phenologies (arrival times) of interacting species (Fig. 1). Second, populations are projected from one year to the next based on their specific demographic rates (e.g., adult longevity, fecundity, etc.). This approach allows one to systematically manipulate mean and variation of relative timing of species phenologies across years and examine the long-term consequences for community dynamics.

Here, I apply this approach to a well-studied two-species Beverton-Holt type competition models (Beverton & Holt 1957). The model describes the change in the population size (N_i) of competing species i and j between two consecutive years ($t \rightarrow t+1$) as:

$$N_{i,t+1} = \frac{\lambda_i N_{i,t}}{(1 + \alpha_{ii} \lambda_i N_{i,t} + f_{ij}(\Delta p_{ij,t}) \lambda_j N_{j,t})} + s_i N_{i,t}.$$

$$N_{j,t+1} = \frac{\lambda_j N_{j,t}}{(1 + \alpha_{jj} \lambda_j N_{j,t} + f_{ji}(\Delta p_{ji,t}) \lambda_i N_{i,t})} + s_j N_{j,t}.$$

with s_i indicating the proportion of adults that survive to the next year. The number of new adults is given by the maximum recruitment rate λ_i in the absence of competition (the product of fecundity of a species and probability of surviving to adult stage in absence of competition) which declines with the sum of intraspecific ($\alpha_{ii} \lambda_i N_{i,t}$) and interspecific ($f_{ij}(\Delta p_{ij,t}) \lambda_j N_{j,t}$) competition. Here, I adjusted the model to reflect common conditions in natural temporary/seasonal communities in nature, where density-dependent regulation from intra- and interspecific competition is largely restricted to offspring (e.g., tadpoles or dragonfly larva in temporary ponds). Thus, the density of the competitor is given by the number of new offspring at the beginning of a year: $\lambda_j N_{j,t}$. However, the model can easily be modified to represent other systems (e.g. annual plant communities Godoy & Levine 2014).

One key innovation here is that the per-capita effect of interacting species, $f_{ij}(\Delta p_{ij,t})$, is a function of relative differences in timing of species' phenologies ($\Delta p_{ij,t}$) (e.g., the number of days between emergence of species i and j within a given year t). Thus, interspecific interaction coefficients are not constant, 'intrinsic' traits of species in a given environment as in classical community models, but instead they are temporally explicit and allowed to vary across years. This modification of interspecific interactions accounts for the fact that changes in relative phenologies typically lead to concurrent changes in per-capita strength of competitive effects in natural systems, without the need to identify the specific underlying mechanisms. Note that the same type of modelling approach can easily be extended to other types of

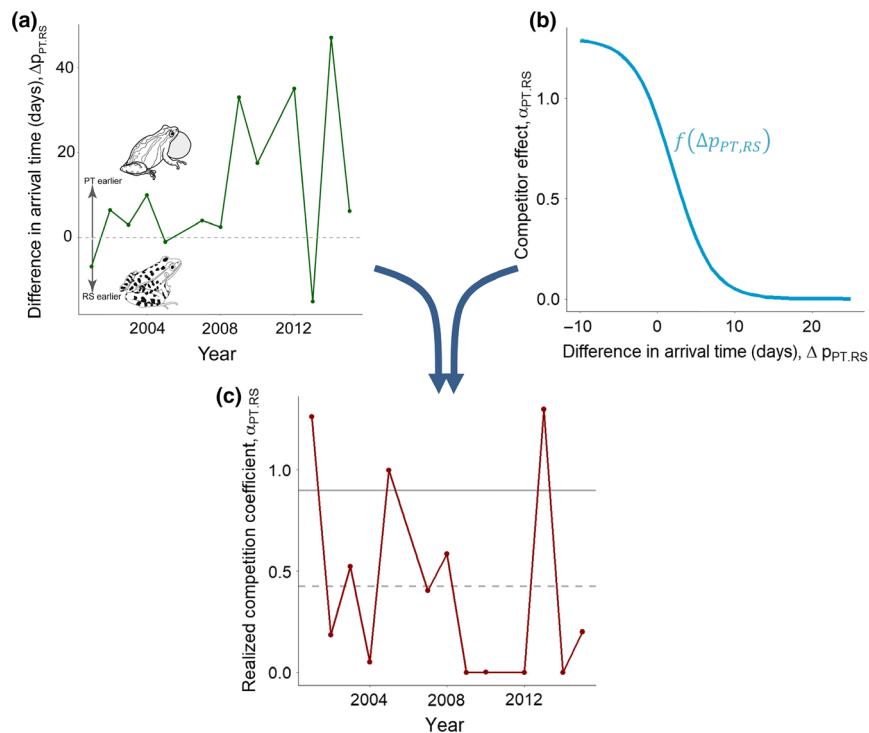


Figure 1 Example of how we can link variation in relative timing of species' phenologies to concordant interannual variation in per-capita interaction strength in natural systems in a few simple steps. (a) In this system, long-term observations reveal considerable interannual variation in mean differences in first calling of Western chorus frog, *Pseudacris triseriata* (PT) relative to its competitor, the Southern leopard frog, *Rana sphenoccephala* (RS). Points indicate mean differences averaged across eight ponds based on 15 years of daily call recordings which are expected to be correlated with differences in relative hatching (arrival) time of tadpoles (b). Subsequent experiments which manipulated the relative hatching time of tadpoles of both species (0, 5, 10, 15, 20 days delay in arrival of RS) were then used to estimate how the per-capita effect of the dominant competitor (RS) affects survival of the inferior competitor (PT). Non-linear curve fitting was then used to derive the competition arrival functions $f(\Delta p)$ (blue line). (c) We can then parameterize the competition–phenology function $f(\Delta p)$ with recorded annual variation in relative arrival times (a) to estimate the realized per-capita effect of *R. sphenoccephala* (RS) on recruitment success of *P. triseriata* (PT) for a given year (solid red line). For reference, solid and dashed grey lines in (c) indicate corresponding per-capita interaction strength predicted when either assuming no difference in phenologies ($\Delta p = 0$) or based on mean differences in first calling date across 15 years, respectively. Data were extracted from (Carter *et al.* 2018; Rudolf 2018). Illustrations by VHWR.

interactions (e.g., predator-prey, mutualistic interactions, parasitism/herbivory, etc.) and to include intraspecific variation in phenology (e.g. Nakazawa & Doi 2012; Revilla *et al.* 2014).

Another advantage of this model formulation is that we can easily parameterize the competition–phenology functions f_j from experiments (Rudolf 2018), which allows us to simulate competitive dynamics for biological realistic conditions and to empirically tests predictions in the future. Figure 1 gives a worked example of how this can be done in a few steps. Furthermore, given a stationary system (i.e., no changes in mean phenologies over time) and no interannual variation in relative phenologies, the difference in arrival time is always the same. In this scenario we can substitute the competition function with a constant: $f_{ij}(\Delta p_{ij,t}) = \alpha_{ij}$, and the model simplifies to a classical competition model (Beverton & Holt 1957; Leslie & Gower 1958) without seasonal dynamics for which the invasion and coexistence conditions are well-understood analytically (Cushing *et al.* 2004).

Theoretically, a variety of relationships of the competition–phenology function $f_{ij}(\Delta p_{ij,t})$ are possible, but biological systems generally fall in two broad categories (Wilbur & Alford 1985; Cleland *et al.* 2015; Clay *et al.* 2019): (1) Early arriver

advantage, where negative effects of interspecific competition on a given species declines the earlier it arrives before others, and (2) late arriver advantage, where negative effects of interspecific competition on a species decrease when it arrives later than its competitors. The effect of shifts in phenologies depends on whether interacting species fall in opposite or the same arrival advantage category. If both species show opposite arrival advantage responses (i.e., one with early one with late arrival advantage), then a shift in relative phenologies will always either increase or decrease ~ the strength of interspecific competition for both species. For instance, consider a hypothetical scenario where species *i* has early arriver advantage and species *j* experiences late arriver advantage. Earlier arrival of species *i* relative to species *j* will increase the early arriver advantage of species *i* and the late arriver advantage of species *j*, resulting in a reduction of interspecific competition for both species. Of course delaying arrival of *i* relative to *j* would result in a negative effect for both species and increase interspecific competition. In systems where this scenario is true, the strength of per-capita interspecific competition coefficients for both species would be positively correlated across a gradient of differences in relative phenologies.

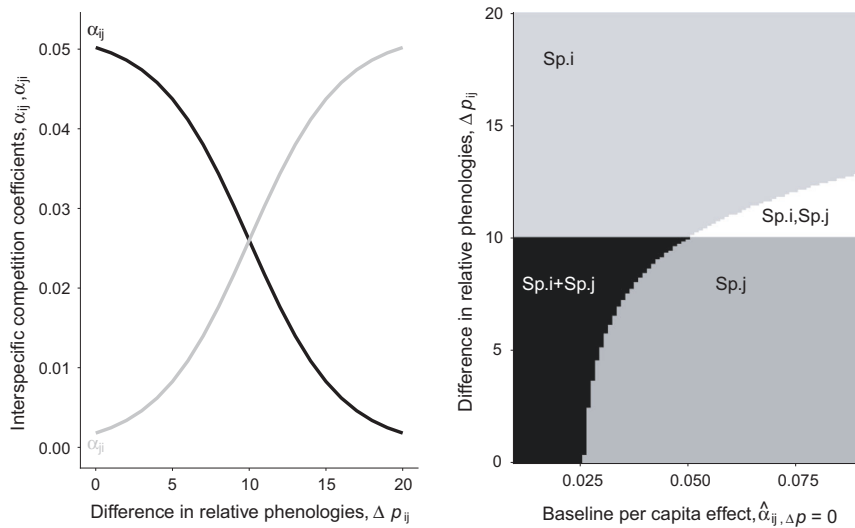


Figure 2 Changes in relative timing of phenologies can fundamentally alter the conditions for coexistence and create novel outcomes and states. Left panels show a numerical example of how strength of per capita intraspecific competitive effects scale with difference in relative arrival (e.g., hatching time) in systems with early arriver advantage for both species. Δp_{ij} indicates the difference in species phenologies (i.e., number of days species i arrives before its competitor, species j). Here, species i is the inferior competitor when both species arrive at the same time as species j ($\hat{\alpha}_{ij,\Delta p=0} = 0.5$ vs. $\hat{\alpha}_{ij,\Delta p=0} = 0.005$). Right panel shows how change in relative arrival time can alter conditions for persistence and coexistence of both species. The x-axis, $\hat{\alpha}_{ij,\Delta p=0}$, indicates the ‘baseline competition coefficient’ when both species arrive at same time ($\Delta p_{ij} = 0$, see ‘Scenario 1’ for detail). In this example, increasing strength of interspecific competition (α_{ij}) can lead to a shift from stable coexistence of both species (black area) to extinction of species i (dark gray). However, a delay in relative arrival time can allow coexistence under a larger range of α_{ij} values. Furthermore, it can result in new outcomes, including counterintuitive extinction of species j , or alternative stable states where either species can be excluded depending on the initial conditions (white area). Outcomes are based on relationships of (α_{ij}) shown in left panel. Note that the sharp transition between system states at $\Delta p_{ij} = 10$ arises because the both competition functions always intersect at that point (see left panel) for all α_{ij} values; if $\Delta p_{ij} < 10$ then $\alpha_{ij} > \alpha_{ji}$, and if $\Delta p_{ij} > 10$ then $\alpha_{ij} < \alpha_{ji}$. Following empirical data (Fig. 1), competition–phenology functions in (a) and (b) were both modelled as sigmoidal functions (see supplement for details), with $A = 0.5$, $x_{mid} = 10$ and $scal_i = -3$, and $scal_j = 3$. Parameters in (b) were: $\alpha_{jj} = \alpha_{ii} = 0.025$, $\lambda_i = \lambda_j = 1.5$, $s_i = s_j = 0$.

Alternatively, if both species show the same type of response (e.g., both perform better when arriving before the other) a delay in relative arrival time will have opposite effects on both species. For instance, with early arriver advantage, a relative delay in arrival of species i decreases the effect of species i on j , but at the same time also increase the effect of j on i . In this scenario, interspecific per-capita interaction coefficients of competing pairs of species (α_{ij}, α_{ji}) are therefore negatively correlated along a relative arrival gradient (e.g., Fig. 2a). However, how quickly the competitive effect increases or declines with difference in relative arrival time (i.e., the slope of $f(\Delta p_{ij,t})$) is likely to differ across species since species can vary in their sensitivities to shifts in relative arrival time (e.g. Stuble & Souza 2016; Rudolf 2018; Alexander & Levine 2019). Note that the same negative correlation and general pattern hold true in systems with late arrival advantage for both species; in this scenario results are simply a mirror images (switched signs) for both species.

Since early arriver advantage is by far the best documented pattern in natural system (Fukami 2015), I largely focus on this scenario for model analyses and numerical simulations. This type of arrival advantage (or priority effect) is well-documented in plant, animal and microbial communities in variety of terrestrial, freshwater and marine systems (Connell & Slatyer 1977; Geange & Stier 2009; Dickie *et al.* 2012; Hernandez & Chalcraft 2012; Kardol *et al.* 2013; Rasmussen *et al.* 2014; Devevey *et al.* 2015; Stuble & Souza 2016; Rudolf

2018; Alexander and Levine, 2019). While a variety of direct and indirect mechanisms can create this effect (Fukami 2015), it commonly arises in seasonal communities due to size-mediated priority effects (sensu Rasmussen *et al.* 2014), which are generated when interactions occur among growing individuals and per-capita interaction strength scales positively with size. It is important to keep in mind that early arriver advantage here refers to per-capita effects and is not driven by numerical effects (e.g., increase in population size over time) as in most classical priority effects models. I will return to this important distinction later in more detail.

DETERMINISTIC INVASION AND COEXISTENCE CONDITIONS

We can gain a first understanding of the model dynamics and importance of the seasonal timing (phenology) of interactions by considering deterministic invasion and coexistence conditions without interannual variation in phenologies (Chesson 2000; Cushing *et al.* 2004). In this system, the growth rate of species j when rare ($j \rightarrow 0$) is given by:

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\eta_j \beta_j}{\left(1 + [\eta_i - 1] \frac{f_{ji}(\Delta p_{ji,t})}{\alpha_{ii}}\right)} + 1 - \beta_j.$$

with $\beta_j = 1 - s_j$, $\eta_i = \frac{\lambda_i}{1-s_i} = \frac{\lambda_i}{\beta_i}$. Using some rearranging, we can show that the growth rate of j is positive, allowing j to

invade from low densities in a single species system with species i present at equilibrium, if,

$$\frac{\alpha_{ii}}{[\eta_i - 1]} > \frac{f_{ji}(\Delta p_{ji,t})}{[\eta_j - 1]}.$$

In other words, a species can invade and persist if the inter-specific competitor (j) has a greater net effect on itself (scaled by its life time reproduction potential: $\eta_j - 1$) than the scaled competitive effects on the invading species for a given phenology. Using the same approach for invasion of species i , this result recovers the equivalent of the well-known conditions in classical Lotka-Volterra type competition models where both species can coexist if:

$$\frac{\alpha_{ii}}{[\eta_i - 1]} > \frac{f_{ji}(\Delta p_{ji,t})}{[\eta_j - 1]} \quad (1)$$

and

$$\frac{\alpha_{jj}}{[\eta_j - 1]} > \frac{f_{ij}(\Delta p_{ij,t})}{[\eta_i - 1]} \quad (2)$$

Finally, if neither species can invade when rare, the outcome depends on the initial relative densities and relative strength of interspecific competition leading to alternative stable states.

TIMING, COMPETITIVE DOMINANCE AND SPECIES COEXISTENCE

Phenologies can affect species interactions and community dynamics in two major pathways: via changes in mean timing of interactions and via changes in interannual variance (i.e., exact seasonal timing differs across years). To isolate the individual and combined effects of both types of phenological change, I divide the analysis in four different scenarios below.

Scenario 1: Shifts in mean phenologies of species interactions

The importance of changes in the relative timing of species' phenologies for coexistence conditions becomes immediately apparent with a bit of re-arranging of eqn 1 and eqn 2. Let us split the competition-phenology functions in two parts: (I) a constant per-capita effect when both species arrive at the same time ($\hat{\alpha}_{ij,\Delta p=0}$), and (II) the degree to which it is modified by a given difference in relative phenologies in a given year t ($\partial_{\Delta p_{ij,t}}$) such that,

$$f_{ij}(\Delta p_{ij,t}) = \hat{\alpha}_{ij,\Delta p=0} + \partial_{\Delta p_{ij,t}} \quad (3)$$

Substituting this formulation into the invasion and persistence conditions above (eqns 1 & 2) immediately reveals a simple but non-trivial fact: we cannot predict competitive dominance and persistence of interacting species without considering the timing (phenology) of interactions and how it affects per-capita interaction strength, i.e., $\partial_{\Delta p_{ij,t}}$ (Fig. 2). For instance, consider a system with early arriver advantage, where $\hat{\alpha}_{ij,\Delta p=0}$ is too large to meet the inequality conditions in eqn 2 when both species arrive at the same time. In this scenario, species i cannot invade and coexist with species j when both phenologies are perfectly synchronized. However, a relative delay in arrival of species j would weaken its per capita

effect (i.e. $\partial_{\Delta p_{ij,t}} < 0$) and thereby decrease the right hand side of eqn 2. This would increase the invasion growth rate of species i and could ultimately allow for its persistence if the delay of j decreases the per-capita effect enough so that inequality in eqn 2 is met, so: $\partial_{\Delta p_{ij,t}} < \frac{\alpha_{ji}[\eta_i-1]}{[\eta_j-1]} - \hat{\alpha}_{ij,\Delta p=0}$. Thus, which species

can ultimately persist and which species will be excluded can switch depending on the relative timing of species' phenologies (Fig. 2). Similarly, some systems may exhibit a stable single species, or coexistence equilibrium, or alternative stable states depending on mean relative phenologies (Fig. 2). Interestingly, these results imply that natural systems with similar species composition and environmental conditions but different mean relative phenologies can have different community dynamics and compositions.

These results also highlight an intuitive but frequently overlooked fact in coexistence studies: species may persist and coexist under conditions that seem implausible if we make predictions based on classical assumption that assume equal phenologies and time-invariant (constant) interaction coefficients. For instance, a species that would be considered competitively dominant (based on same arrival times) may be excluded from the system if its phenology is delayed relative to its competitor (Fig. 2). Thus, competitive dominance in seasonal systems should ideally be discussed in the context of species' relative timing of phenologies.

The same conceptual framework outlined above also allows us to make some predictions about how phenological shifts will affect species interactions and community structure. If the timing of interactions can determine their outcome, this also implies that shifts in mean phenologies (e.g., due to climate change), could alter the persistence and coexistence conditions of natural communities. Whether a shift in relative phenologies ultimately promotes or demotes coexistence of competing species depends on the competitive asymmetry and the direction of the shift, i.e., whether it favours the competitively inferior species. For instance, with competitive asymmetry and early arriver advantage (see above), a long-term phenological shift delaying arrival of the dominant competitor should facilitate coexistence (Fig. 2), especially if the dominant species is less sensitive to this shift (i.e., shallower slope of $f(\Delta p)$). In this scenario, phenological shifts would serve as both an 'equalizing' mechanism and potentially also as a 'stabilizing' mechanism (sensu Chesson 2000). It would be equalizing because it reduces the competitive asymmetry between species by weakening the effect of the dominant species and enhancing the effect of the inferior species. It could be stabilizing if it also increases the sum of both right hand sides of invasion conditions (eqns 1 & 2) and thus increase the invasion rate of both species when rare. In contrast, if both species are competitively very similar, then increasing differences in phenologies would result in competitive asymmetry and thus reduce the potential for coexistence (reducing 'equalizing' mechanisms), regardless of which species is delayed.

Scenario 2: Variation in relative timing of phenologies across years

Relative timing of species' phenologies naturally vary across years, and this variation differs across systems. For instance,

a species may hatch/emerge earlier than its competitor, at the same time, or even later depending on the year (e.g., Fig. 1). Whether and how this variation affects short- and long-term dynamics of interactions ultimately depends on whether the relationship between interaction strength and relative timing of phenologies ($f(\Delta p)$) is linear or non-linear. If the competition–phenology relationship is linear, then the long-term term average is simply the mean competition coefficient at the average difference in phenologies: $\overline{f_{ij}(\Delta p_{ij,t})} = f_{ij}(\overline{\Delta p_{ij,t}})$. In this scenario variation will not alter the average per-capita interaction strength or equilibrium coexistence conditions of the system.

Recent studies indicate, however, that interaction strength can scale non-linearly with difference in relative phenologies (Rudolf 2018). Indeed, such non-linear relationships are expected to be the norm in natural systems where interactions occur between growing individuals and can arise through a number of different mechanisms (e.g., due to positive feedbacks and/or non-linear growth rates). By Jensen's inequality (Jensen 1906), a non-linear relationship implies that interannual variation can modify the interaction strength (Rudolf 2018). Specifically, it can either increase or decrease the average interaction strength (non-linear averaging effect), depending on whether the monotonic curvature of the relationship around the mean phenologies is convex, $\frac{\partial^2 f_{ij}}{\partial \Delta p_{ij}^2} > 0$, or concave, $\frac{\partial^2 f_{ij}}{\partial \Delta p_{ij}^2} < 0$, respectively. The stronger the non-linearity, the stronger the effect of interannual variation becomes (e.g., $\Delta p_{ij} = 15$ vs. $\Delta p_{ij} = 5$ in Fig. 3a). Interestingly, this also indicates that populations with the same mean phenologies but different levels of interannual variation in relative phenologies will have different average interaction strengths.

By altering per-capita interaction strength, interannual variation can also fundamentally alter the outcome of species interactions and potential for species' persistence and coexistence. Indeed, just like changes in mean phenologies, changing phenological variation in a system can alter the possible outcomes (states) in a given system, e.g., it can reverse competitive dominance and exclusion, allow for stable coexistence, or introduce alternative stable states. We can predict these qualitative effects on coexistence by considering several distinct biological scenarios (summarized in Table 1). First, consider a system where the competition–phenology functions f_i have the opposite curvatures for both species across relative phenologies. In this scenario, interannual variation can facilitate coexistence if the competition function is concave down ($\frac{\partial^2 f}{\partial \Delta p^2} < 0$) for the dominant/stronger competitor (see Fig. 3a for $\Delta P < 10$) because variation reduces the average negative effect of the dominant competitor, thereby increasing the invasion rate of the inferior competitor when rare (e.g., Fig. 3c). Furthermore, variation will also increase the competitive effect of the weaker competitor on the dominant competitor, thereby reducing differences in interspecific competition (equalizing effect) (Fig. 3b). If the effect is strong enough to reduce the right side of eqn 1 and/or eqn 2, then increasing variation can also lead to long-term coexistence (stabilizing effect) (Fig. 4). Of course, the opposite is true (i.e., decrease in coexistence potential) if the curvature is convex ($\frac{\partial^2 f}{\partial \Delta p^2} > 0$) for the dominant competitor (see Table 1, Fig. 3 for $\Delta P > 10$).

Finally, we could encounter a scenario where the curvatures of competition–phenology functions are the same for both species (Table 1). If both curvatures are concave, this will reduce strength of interspecific competition for both species and increase invasion rates of either species when rare. Thus, variation can potentially promote coexistence in this scenario if the effect is strong enough to reduce the right side of eqns 1 and 2 (stabilizing effect). The opposite is true if both curvatures are convex. Overall, these results suggest that interannual variation could be an important, yet overlooked mechanisms promoting species coexistence, especially given that this type of variation is ubiquitous in natural systems (Pearse *et al.* 2017; Rudolf 2018).

Scenario 3: Stochasticity and transient community dynamics

The previous analyses focused on invasion growth rates under equilibrium conditions and thus does not account for transient dynamics and systems where species are not at equilibrium. Indeed, many systems never reach an equilibrium state or may exhibit complex alternative states (Hastings *et al.* 2018). To examine how interannual variation in phenologies affect the transient dynamics and structure of such systems and numerically test analytical predictions, I simulated stochastic community dynamics by allowing differences in relative phenologies to vary across years (see Supplement for simulation details). Overall, simulations show that interannual variation can introduce alternative stable states: instead of one species always winning for a given parameter combination, it is possible that both species coexist (Fig. 1) or that either one of the species can competitively exclude the other one. These alternative stable states are more likely the more similar the competitive abilities of both species are and the larger the interannual variation is. Which species ultimately wins in these scenarios depends on the temporal sequence of relative phenologies and baseline life-history traits. For instance, if, by chance, the weaker competitor arrives repeatedly earlier than its dominant counterpart, it can gain a sufficient advantage that may ultimately allow it to persist and outcompete its competitor.

These alternative states do not arise from differences in initial densities as in classical deterministic competition models. In these models, priority effects arise if (1) the system is in a parameter space where alternative stable states occur based on a given set of per-capita interaction coefficients, and (2) differences in arrival time at a given patch lead to concurrent differences in densities when interactions are initiated (i.e., early arriving species has time to increase in population size before late arriver appears) (Schoener 1976; Case 1990; Vasseur *et al.* 2011; Fukami *et al.* 2016; Ke & Letten 2018). Instead, they arise here because differences in relative phenologies lead to concomitant changes in per-capita effects. Numerical priority effects still possible in this system, but they depend on the per-capita effects and thus relative arrival time of species (i.e., they can only occur in white region in Fig. 2).

Finally, variation can also strongly decrease the time to extinction of a given species and potentially even lead to stable long-term coexistence (Fig. 4). Ultimately, the positive effects of interannual variation on persistence and coexistence

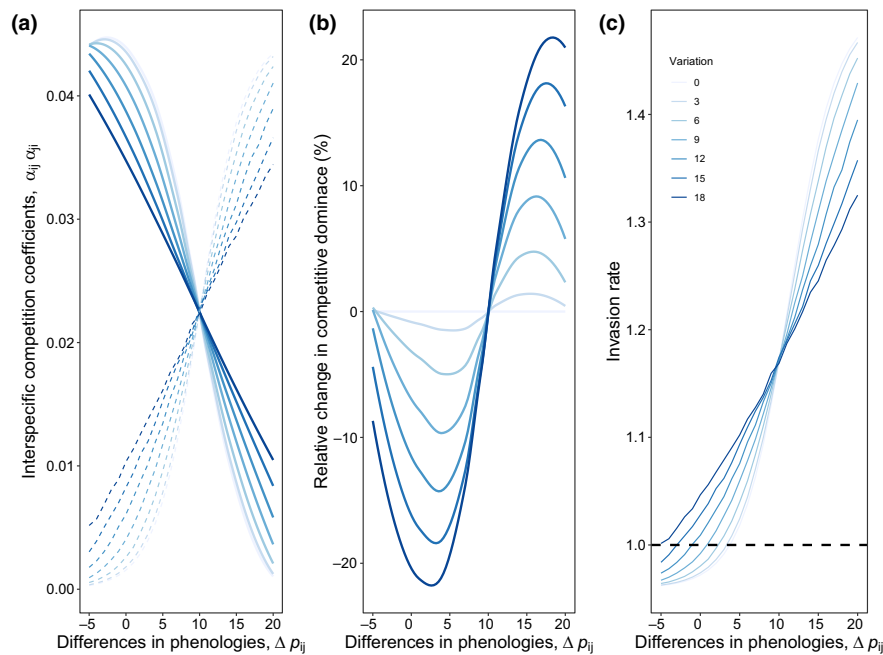


Figure 3 Example of how interannual variation in relative timing of phenologies can change per-capita competition effects, competitive asymmetry, and invasion rate of the inferior competitor if the competition–phenology function, f_{ij} , scales non-linear with differences in relative phenologies (e.g., hatching time). Δp_{ij} indicates the number of days species i arrives before its competitor, species j . (a) per-capita interspecific interaction coefficient for species j on species i (α_{ij} , solid lines) and vice versa (α_{ji} dashed lines) assuming early arriver advantage for both. (b) Proportional change in competitive dominance. Negative values indicate reduction and positive values increase in competitive asymmetry (i.e., dominance of species j) relative to the no-variance control scenario. (c) Invasion growth rate of inferior competitor, species i , into population of species j at equilibrium density. The invasion rate has to be > 1 (dashed black line) for successful invasion (and thus persistence) of species i . In this scenario, increasing variation can facilitate invasion and persistence of species i with small differences in arrival time because of the concave curvature of the competition function α_{ij} in (see panel a). In all panels, different line colours indicate average interaction strength for different levels of simulated interannual variation in arrival time around a given mean based on 9900 simulations (see Supporting Information for simulation details). Variation indicates absolute difference in relative arrival days assuming uniform distribution with a range twice the average (no variation = 0). Parameters are: $A = 0.5$, $x_{mid} = 10$ and $scal_i = -3$, and $scal_j = 3\lambda_i = \lambda_j = 1.5$, $s_i = s_j = 0$, $\alpha_{ji} = 0.04$.

are contingent on the curvature of the competition functions around the mean (see Scenario 2, Table 1). Overall, these patterns are consistent with the deterministic analyses above and driven by the same underlying mechanisms: changes in per-capita interaction strength.

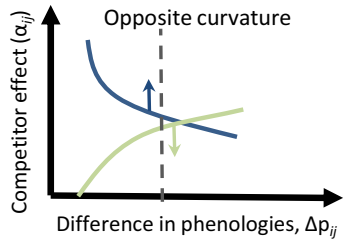
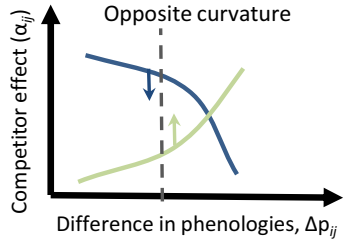
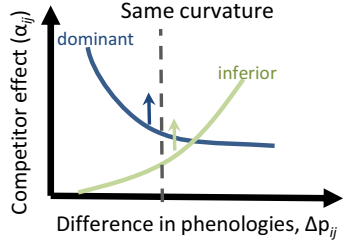
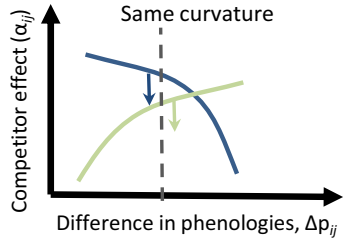
Scenario 4: Non-stationary systems and the interactive effect phenological mean and variance

So far, we have considered stationary systems where the mean and variance are constant across years. However, climate change is altering the differences in mean phenologies of species around the world, effectively creating non-stationary systems (Wolkovich *et al.* 2014). The model and analyses described above also provide a simple and intuitive framework of predicting how these non-stationary changes will affect communities. For instance, without interannual variation, we can directly predict the outcome of these shifts in mean phenologies as explained in Scenario 1 (e.g., by moving along the y axis in Fig. 2). How sensitive a system is to changes in mean phenologies will depend on the slope of the competition–phenology function $f(\Delta p)$: a shallow slope around the current mean will result in little change in per-capita effects, while a steep slope implies that even small shift in

mean phenologies can lead to dramatic changes per capita effects and population densities and thus is more likely to alter the persistence/coexistence potential.

Most systems also exhibit natural interannual variation in phenologies, and this variation can alter the net effect of non-stationary changes in mean phenologies, i.e., the rate at which the system changes. The direction and magnitude of this modification effect again depends on the curvature of the competition–phenology function $f(\Delta p)$ around the mean: the effect of changing mean phenologies will either be smaller or larger than expected if the curve is concave or convex respectively. As a consequence, the system may change slower (or faster) than expected (e.g., Fig. 5) and this effect increases the stronger the curvature of the function. In many systems, mean and the interannual variation in phenologies will both change at the same time, and this can either enhance or delay the negative (or positive) effects of shifts in the mean if the competition–phenology function $f(\Delta p)$ is non-linear (see above). Overall, these results highlight the importance of interannual variation in phenologies for mitigating the rate at which systems change in response to continuous climatic change. They also indicate that phenological shifts can have variable, but predictable effects on a system that can be inferred from a general understanding of how per-capita interaction strength

Table 1 Effect of interannual variation on coexistence potential

Curvature of competition—phenology function $f(\Delta p)$	Variance effect on α_{ij}, α_{ji}	Competitive asymmetry	Coexistence potential
Dominant: Concave up Inferior: Concave down 			
Dominant: Concave down Inferior: Concave up 			
Dominant: Concave up Inferior: Concave up 			
Dominant: Concave down Inferior: Concave down 			

The curvatures of the competition–phenology function of dominant and inferior competitor around a given mean (dashed vertical line) determines whether increasing variation in timing of interactions across years will either promote or demote the potential for coexistence. Vertical dashed lines show mean difference in phenologies across years, curves show different scenarios of competition–phenology function combinations for two competing species. Arrows indicate qualitative, directional effects of increasing interannual variation on the strength of interspecific competitive effects (α_{ij}, α_{ji}), competitive asymmetry (absolute differences between α_{ij}, α_{ji}) and the potential for coexistence. Colours correspond to species specific competitive effects and functions.

scales with differences in timing of relative phenologies, i.e., the slope and curvature of the competition–phenology function.

Limitations and extensions

The analysis above shows that shifts in relative timing of phenologies alone can change coexistence conditions by altering per-capita interaction strength. These changes can occur even if phenologies track optimal environmental conditions (i.e., conditions remain mostly constant across differences in relative phenologies). However, in some systems, shifts in the relative timing of interactions may also be correlated with

changes in environmental conditions that influence other demographic parameters. For instance, a suboptimal shifts in a species phenology could expose individuals to different and potentially detrimental environmental conditions (e.g., lower temperatures or resource abundance), thereby reducing their reproduction or survival (i.e., reduce λ in eqn 1 & 2). In this scenario, changes in per-capita interaction strength mediated by shifts in relative timing of phenologies could be correlated with changes in other key demographic rates.

We can gain a general understanding of how environmental changes might interact with phenological shifts to influence outcome of species interactions using the modelling approach outlined above. I will use λ as an example here, but the same

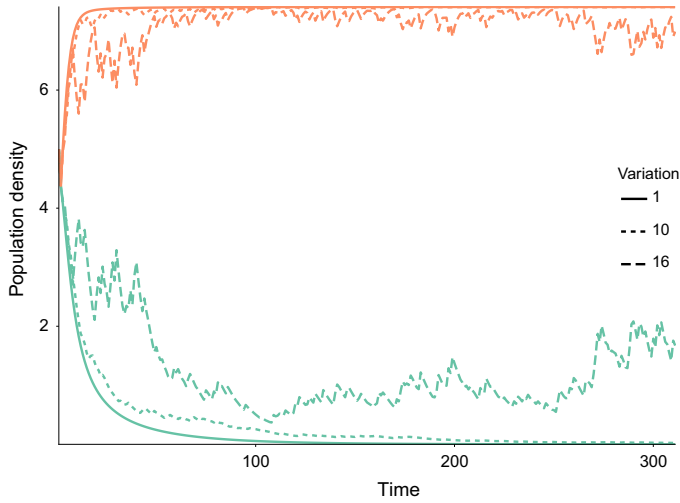


Figure 4 Population dynamics under different levels of interannual variation in relative timing of phenologies. With negligible interannual variation, species *i* (blue lines) is quickly competitively excluded by species *j* (orange lines). Increasing variation reduces the time to extinction of species *i*, and high enough variation allows for long-term coexistence of species *i* and *j*. $\alpha_{ji} = \alpha_{jj} = 0.045$, $\alpha_{ij} = 0.05$, $\Delta p_{ij} = 0$; values and competition–phenology functions correspond to Fig. 3 above. Variation indicates absolute difference in relative arrival days assuming uniform distribution with a range twice the average. Means are average of 9900 stochastic simulations (see Supporting Information for details).

steps can be applied to other life-history traits. We can describe the relationship of λ and phenological shift as: $\lambda_i = \hat{\lambda}_i + \Delta_{\lambda i, t}$, where $\hat{\lambda}_i$ is the value of λ for species *i*

when both species arrive at the same time ($\Delta p = 0$), and $\Delta_{\lambda i, t}$ is the degree to which it is changed by a given shift in the phenology of species *i*. Note, that unlike per capita interaction strength (e.g., α_{ij}) the change in λ (i.e., $\Delta_{\lambda i, t}$) is independent of the phenology of other species; instead it is a function of the change in environmental condition the focal species experiences. This distinction is important because it emphasizes different underlying mechanisms that may or may not be correlated. Substituting this expression into eqn 3, we obtain the invasion conditions for species *j*:

$$\frac{\alpha_{jj}}{\left[\frac{\hat{\lambda}_j + \Delta_{\lambda j, t}}{\beta_j} - 1 \right]} > \frac{\hat{\alpha}_{ij, \Delta p=0} + \partial_{\Delta p_{ij, t}}}{\left[\frac{\hat{\lambda}_i + \Delta_{\lambda i, t}}{\beta_i} - 1 \right]} \quad (4)$$

eqn 4 indicates that changes in λ mediated by an absolute shift in species' phenologies can alter coexistence conditions and the result will depend on: (1) how this shift in λ is correlated across both species (i.e., the ratio of $\Delta_{\lambda j, t}$ and $\Delta_{\lambda i, t}$), and (2) how this ratio in turn is correlated with shifts in interspecific per capita interaction strength, $\partial_{\Delta p_{ij, t}}$. The first relationship is straight forward: if phenological shifts increase λ of the competitor more than λ of the invader, the invasion conditions in eqn 4 is harder to meet, reducing the potential for the invader to persist. The relationship between $\frac{\Delta_{\lambda j, t}}{\Delta_{\lambda i, t}}$ and $\partial_{\Delta p_{ij, t}}$ describes how the effect of changes in environmental conditions are correlated with the effect of changes in relative timing of phenologies. If both are positively correlated (e.g., shift decreases relative λ of the competitor and its competitive per-capita effect, so $\partial_{\Delta p_{ij, t}} < 0$ and $\frac{\Delta_{\lambda j, t}}{\Delta_{\lambda i, t}} < 1$), then their effects are synergistic and shifts in the relative timing of phenologies will have larger than expected effects solely based on shifts in per-

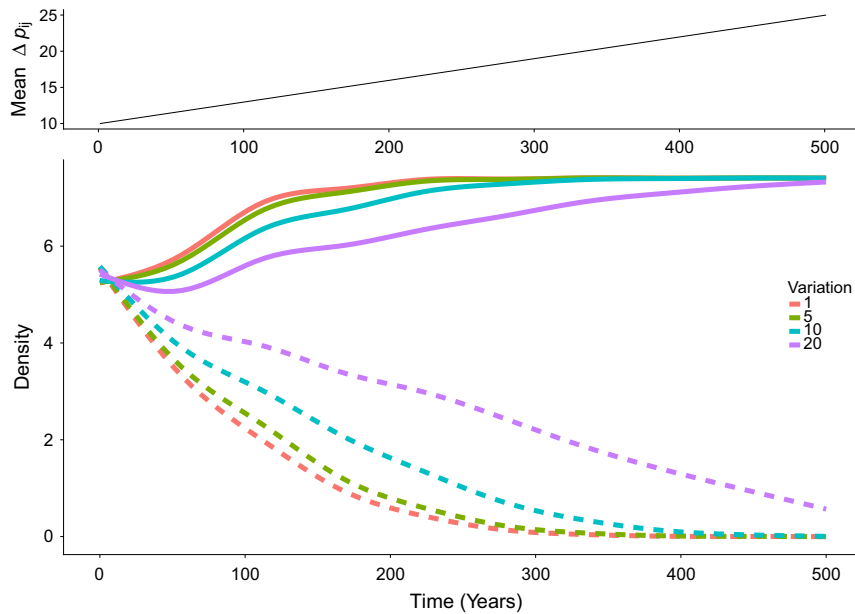


Figure 5 Consequences of non-stationary, continuous shift in relative timing of phenologies (Δp_{ij} shown in top panel) on densities of two competing species. Colours indicate level of interannual variation in arrival time (in days) around a given mean (see Fig. 4) and lines indicate mean densities smoothed across repeated stochastic simulations ($N = 100$) to highlight temporal trends (see Supporting Information for details). Solid lines = early arriver *i*, dashed = late arriver *j*. Here, shift in arrival time has smaller effect on both species with higher level of variation, slowing down and extending time to extinction of later arriving competitor (dashed lines). E.g., populations decline > 54% in first 100 years in absence of interannual variation, but decline only by 14% with 20 day interannual variance which also delays extinction by centuries. Competition and arrival function follow those in Fig. 3 with parameters: $A = 0.5$, $x_{mid} = 10$ and $scal_i = -3$, and $scal_j = 3\lambda_i = \lambda_j = 1.5$, $s_i = s_j = 0$, $\alpha_{jj} = 0.045$.

capita interaction strength. In contrast, a negative correlation between $\frac{\Delta_{ij,t}}{\Delta_{ii,t}}$ and $\partial_{\Delta_{ij,t}}$ (e.g., relative increase in λ of competitor but decrease in its per capita competitive effect) would result in antagonistic effects of both types of shift, thereby reducing or potentially reversing the effect predicted solely based on changes in interaction strength.

Unfortunately, we know little about which correlations are more likely to occur in natural systems, and the details are likely to be system specific. However, once the relationships are established for a given system, the example above demonstrates how we can easily account for such system specific details to predict the net effect of phenological shifts on persistence and coexistence in a given system. Indeed, this approach could be used in future studies to compare the importance of changes in environmental conditions vs. species interactions associated with phenological shifts. Regardless of these system specific details, the underlying mechanism remain the same: phenological shifts can alter outcome of species interactions and either promote or demote coexistence via their effect on competitive (as)symmetry.

Finally, the model assumes that phenologies in one year are independent of phenologies in the previous year. This is a common assumption in phenology models (Nakazawa & Doi 2012; Revilla *et al.* 2014) and a good first approximation for many systems where phenologies are largely driven by year specific seasonal cues (e.g., temperature or rain), but it may not hold true in multivoltine systems. For instance, changes in competition due to phenological shifts can influence developmental rates and thus the phenology of next life stage (Carter & Rudolf in review). However, we currently have little information on when and how the timing of phenologies is correlated across life-stages or generations and more data is needed before we can make biological realistic models to examine how this might affect coexistence patterns.

DISCUSSION

The phenology of species interactions is increasingly recognized as a major force structuring natural communities, but studies on phenologies and coexistence theory have largely proceeded independently. The theory outlined here was specifically developed to help make this connection. Overall, the model revealed that the conditions for species coexistence and persistence could strongly be influenced by the relative timing of species' phenologies and the outcome depends on how per-capita interaction strength scales with this timing, i.e., the shape of the competition–phenology function. As a consequence, any differences or shift in mean relative timing of species' phenologies (e.g., due to climate change) has the potential to fundamentally alter persistence and coexistence conditions. Furthermore, the model also reveals that interannual variation in species phenologies play an equally important role in driving long-term and transient dynamics of communities, and could be a ubiquitous, but currently neglected mechanism facilitating species coexistence. Overall, these results highlight that shifts in phenology of species interactions can lead to variable yet predictable changes in coexistence potential in competitive systems, emphasizing the need for temporally explicit coexistence theory in a changing world.

UNDERSTANDING SPECIES COEXISTENCE – WHEN AND WHY DO WE NEED TO ACCOUNT FOR PHENOLOGY?

The importance of timing for coexistence

Identifying the mechanisms which promote or demote the potential for a species to persist and coexist with other members of the community has been a perennial challenge in ecology (Hutchinson 1961; Chesson 2000; Levine *et al.* 2017). Overall, the model outlined here emphasizes that seasonal timing of interactions can be an important mechanism that drives coexistence patterns in natural systems. However, how does it fit into existing concepts of coexistence theory? One might be tempted to equate the relative timing of interactions to spatial overlap of niches, assuming that larger temporal differences will decrease the 'temporal niche overlap' among species (Wolkovich & Cleland 2011). However, this is often misleading because time is unidirectional, i.e., it can only move in one direction. Thus, unlike space, relative positions on the time axis are not interchangeable. For instance, if two species are increasingly separated in space, their impact on each other is going to decrease for both. In contrast, envision a system with early arriver advantage. In this scenario, changing the timing of species, e.g., by advancing the phenology of one species relative to the other, will reduce the per-capita effect of the late arriver on the early arriver, but it will also increase the negative effect on the late arriver. Clearly, once the differences in species' phenologies are large enough, interaction strength might eventually decrease, e.g., if the early arriver has left the community (e.g., due to metamorphosis) and the limiting shared resource has enough time to be renewed. However, such temporal priority effects of species with early phenologies can persist for substantial periods of time and does not necessarily correlate with temporal overlap (co-occurrence) of competitors in natural systems (e.g. legacy effects Wilbur & Alford 1985; Grman & Suding 2010; Rudolf & Van Allen 2017). Furthermore, effects may not decrease over time, but could become stronger, e.g., due to 'niche modification' (Fukami 2015). So a shift in timing by itself will not necessarily reduce niche overlap or always promote coexistence. Indeed, it can just as well decrease the potential for coexistence. Hence, it should not be surprising when phenological differences reduce the potential for coexistence in some systems (Kraft *et al.* 2015). Ultimately, the outcome can only be inferred from a detailed understanding of how per-capita effects scale with timing (phenology) of interactions.

Modern coexistence theory has played a particularly important role in highlighting the importance of temporal variation (Chesson 1994; Chesson 2000; Godoy & Levine 2014; Ellner *et al.* 2016; Barabás *et al.* 2018). At its core, it focuses on two non-independent determinants of coexistence: 'equalizing' mechanisms that determine competitive advantage of species, and 'stabilizing' mechanisms which allow populations of species to increase (i.e., invade) when rare in the community. The effects of timing on coexistence in the current model can be condensed to a simple driving mechanism: its effect on competitive (i.e., per-capita effect) asymmetry between species which affects both equalizing and

stabilizing mechanism (Fig. 6). Simply put, if differences in relative phenologies (timing) reduce differences in interspecific per-capita effects, then they will decrease competitive asymmetry and thereby increase equalizing mechanisms. For instance, shifting the timing in systems with existing competitive asymmetry in favour of the inferior competitor can promote coexistence, because it reduces the competitive asymmetry, thereby reducing differences in competitive dominance (Fig. 6). The model also shows that changes in interaction coefficient due to phenological shift can also change invasion growth rate of species when rare, indicating that phenological shifts can also affect stabilizing mechanisms. Thus, the timing of species interactions is an important driver of species coexistence that fits well within the existing frameworks of coexistence theory.

Interannual variation in phenologies as a coexistence mechanism

Temporal variation is increasingly recognized as an important factor influencing species coexistence (Chesson 2000; Barabás *et al.* 2018). For instance, external fluctuation (Chesson 1994; Chesson 2000) (e.g., due to temperature, precipitation) or endogenous fluctuations (Armstrong & McGehee 1980; Huisman & Weissing 1999; Abrams & Holt 2002; Kuang & Chesson 2008) can alter the potential for coexistence under certain conditions when they affect

demographic rates or population densities of competitors differentially. However, variation in the timing of interaction has received little attention in this context. This is surprising given that variation in the timing of interactions is nearly ubiquitous in nature and frequent in aquatic and terrestrial systems across a wide range of taxa (Saenz *et al.* 2006; Ellebjerg *et al.*, 2008; Høye & Forchhammer 2008; Iler *et al.* 2013; Youngflesh *et al.* 2018). Here, I show that variation in the timing of interactions can play a key role in driving outcome of species interactions, and under some conditions, it can even promote coexistence. Interannual variation in the timing of interactions can affect coexistence conditions through a range of mechanisms. First, if the interaction strength scales nonlinearly with phenologies, variation has always the potential to change the strength of interactions due to non-linear averaging. This change can promote coexistence if it benefits the inferior competitor and thereby reduces competitive asymmetry in the system. Second, species will almost certainly differ in the shape of this function (e.g., due to differences in life history traits like growth rates, initial body size, etc.). Thus, species will respond differentially to interannual variation in timing, leading to temporal relative non-linearity which can facilitate coexistence under certain conditions (Chesson 2000).

Which of these different mechanisms will affect coexistence conditions and their relative importance will ultimately

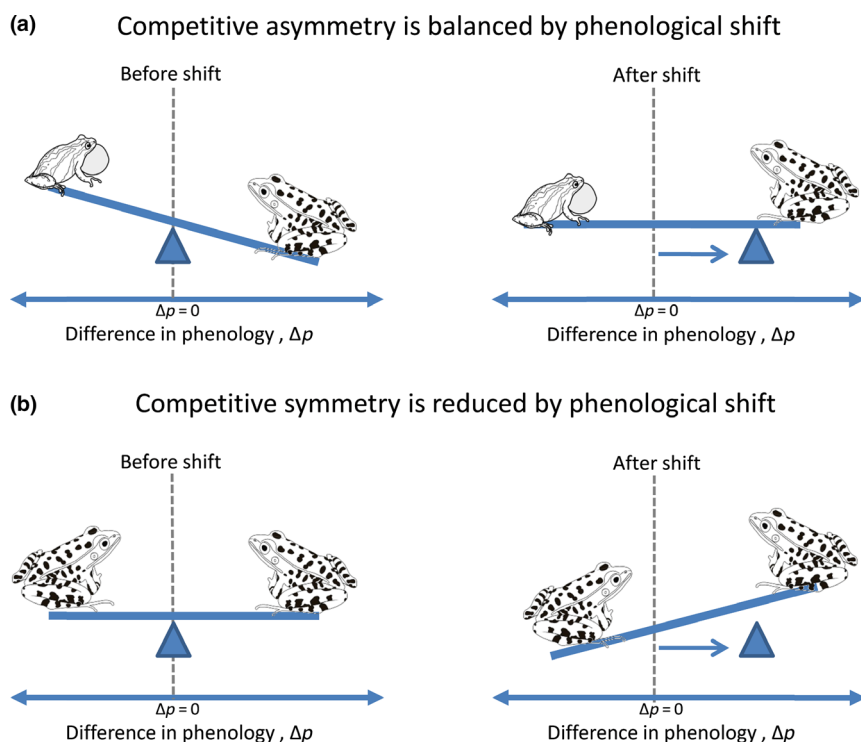


Figure 6 Potential effects of phenological shifts on competitive balance. (a) shows a scenario where one species (right hand side) is competitively dominant when both species arrive at same time (indicated by dashed vertical line). A shift in relative timing of phenologies resulting in delay of the competitive dominant species can increase or even restore competitive symmetry by reducing effect of dominant competitor. (b) shows a scenario where both species have similar competitive abilities when both phenologies are aligned. Here, a phenological shift can result in competitive asymmetry and reduce coexistence potential. Triangle tip indicates relative difference in timing of specie' phenologies, arrows indicate shift in mean phenologies. Image size of species represents competitive ability (larger = competitive dominant) in absence of phenological differences. Illustration made by V.H.W.R

depend on the specifics of the system and how interaction strength scales with relative timing of phenologies for interacting species. The theory presented here indicates that the seasonal timing of interactions is likely an important yet currently neglected driver of species coexistence that fits well within existing concepts of coexistence theory and emphasizes the importance of taking a temporally explicit approach to community ecology that accounts for sequence of phenologies in natural communities.

Priority effects in seasonal communities

There is a clear connection between phenological shifts in the timing of species interactions and the classical concept of priority effects. Priority effects arise when differences in the assembly history alter the effects of species on one another and play a key role in structuring natural communities (Chase 2003; Fukami *et al.* 2016). The ‘effect’ of a species on another can be separated in two interacting components, per-capita interaction strength, and the number of interacting individuals. Previous theory has largely focused on priority effects via changes in numbers and rarely considers priority effects via changes in per-capita interaction strength (with the exception of evolutionary priority effects (e.g. Urban & De Meester 2009; De Meester *et al.* 2016)). Yet, there is a rich body of empirical work demonstrating that differences in arrival time (phenology) within a season can alter outcome of interactions within a generation even in the absence of any numerical effects (Geange & Stier 2009; Hernandez & Chalcraft 2012; Kardol *et al.* 2013; Rasmussen *et al.* 2014; Rudolf 2018; Alexander & Levine 2019). In these studies, priority effects are typically mediated by changes in traits (e.g., via behaviour or size) that directly or indirectly (e.g., via ‘niche modification’ (Fukami *et al.* 2016)) determine per-capita effects. Importantly, trait mediated changes in per-capita effects can lead to alternative stable states, but they can also lead to long-term changes in relative abundances of species, an outcome not-expected from traditional numerical priority effects. This emphasizes the importance of distinguishing between both types of priority effects since they tend to operate at different time scales (within vs. across generations) and result in different long-term effects. Given that shifts in the timing of species’ phenologies are widespread and expected to influence per-capita effects, this suggest that trait-mediated priority effects are common but understudied driver of the dynamics and structure of natural communities. More theory is needed to generalize the role of timing-varying interaction strength in driving long-term dynamics.

PRACTICAL IMPLICATIONS – HOW TO MEASURE INTERACTION STRENGTH TO PREDICT COMMUNITY DYNAMICS IN THE REAL WORLD

The strength of species interactions is at the heart of all coexistence theory and is required to make predictions about the current and future state of an ecological community. The analyses presented here suggest that we need to carefully rethink how we quantify interaction strength to make these predictions. Traditionally, interaction strength has been

inferred either from natural patterns or from controlled experiments. Controlled experiments are efficient because they can quantify per capita interaction strength across a range of densities and/or conditions (e.g., surface response designs) (Inouye 2001). However, the default is to keep phenologies constant and often synchronized, e.g., two competing species are introduced to the experiment at the same time (but see studies on priority effects (Fukami 2015)). This approach would lead to misleading predictions for a natural system if phenologies are not perfectly aligned, i.e., our experimental estimates would not represent realized interaction strength in nature and we would end up looking at the wrong coexistence parameter space. In contrast, estimating interaction strength from natural systems will inherently account for any natural differences in the timing of species’ phenologies and thus provide the ‘realized’ interaction strength. While experiments could be adjusted to account for this natural difference, both approaches are likely to provide inaccurate estimates if timing naturally varies across years. More importantly, neither approach can be used to predict dynamics outside the range of current mean and variance. This dramatically hampers our ability to accurately predict how any changes in mean timing of phenologies will affect the focal species or coexistence patterns, or infer how variation across years impacts the system.

We can only overcome these limitations, avoid potential erroneous conclusions and gain reliable prediction on how changes in species phenologies affect natural systems, if we have a good understanding of how differences in relative phenologies of species affect per-capita interaction strength (i.e., competition–phenology function/ $f(\Delta p)$). This can be either achieved using observational or experimental approaches that link a wide range of relative phenologies to the per capita interaction strength (Yang & Rudolf 2010). Overall, the same tools and designs can be used that are already applied to link other environmental or density gradients to per capita effects (Inouye 2001; Inouye 2005). For instance, we can experimentally create a gradient of relative phenologies to estimate the shape of the competition–phenology function for a range of species pairs (Lawler & Morin 1993; Yang & Rudolf 2010; Rudolf 2018; Alexander and Levine, 2019). Similarly, we can examine the correlation between phenological differences and estimates of interaction strength from natural patterns if we have multi-year observations with a wide range of phenologies. Note that if phenological shifts modify per-capita interactions among multiple generations, these designs and analyses need to account for the natural age/size structure present in the competitor.

Findings presented here emphasize the importance of the competition–phenology function to predict coexistence of species and how these communities will change if phenologies change. Unfortunately, we currently have few empirical estimates for any of these relationships (e.g. Farzan & Yang 2018; Rudolf 2018; Alexander & Levine 2019). Even studies on priority effects typically use before/after type treatments or arrival order instead of an arrival time gradient (Alford & Wilbur 1985; Hernandez & Chalcraft 2012; Stier *et al.* 2013; Tucker & Fukami 2014; Cleland *et al.* 2015; Rudolf & McCrory 2018), and thus cannot be used to infer importance of interannual variance or make predictions about how changes in mean arrival time affect species.

Increasing the number of studies that examine the competition–phenology function across a wide range of taxa and environmental conditions will be imperative to develop general expectations for a larger range of systems. Importantly, they will also help us to determine what factors influence the shape of the competition–phenology relationship. For instance, if interactions occur among growing individuals and are driven by size, then the shape of the competition–phenology function will vary with any factor that alters the growth rates of interacting species (e.g., temperature or resource productivity)(Rudolf 2018). Clearly, we cannot estimate the competition–phenology function for all interactions of interest (just as we cannot estimate all competition–density relationships), but if we have a general understanding of what factors determine the relationship, we can model the relationship as a function of environmental conditions and use general rules of thumb to make qualitative predictions (e.g., Table 1). Such an approach would vastly improve our ability to understand the factors that promote species coexistence and ultimately maintain biodiversity across systems and help to predict when climate mediated shifts in species' phenologies will have positive or negative effects on natural communities.

CONCLUSIONS

Traditional coexistence theory does not account for seasonal timing of interactions. As a consequence, per capita interactions are implicitly assumed to be constants. If species' phenologies would always be perfectly aligned and constant across time and space or outcome of interactions are independent of timing, this would not be an issue. Alas, this is not the case for most natural systems. Furthermore, climate change continues to change the temporal structure of natural communities and creates non-stationary systems. These patterns challenge the core assumption of many traditional community models and supports recent calls for developing temporally explicit framework to community ecology (Wolkovich *et al.* 2014). The work presented here is an important step in this direction, but much work remains to be done. It also indicates that taking a temporally explicit approach in future empirical and theoretical studies will provide a fruitful venue to gain new insights into the basic mechanisms that drive the structure and dynamics of natural communities.

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DATA AVAILABILITY STATEMENT

No new data was used.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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